# Interactive community responses to disturbance in streams: disturbance history moderates the influence of disturbance types

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**Abstract**

Both disturbance history and disturbance type act to structure communities through selecting for particular species traits but they may also interact. For example, flooding selects for species with flood-resistant traits in streams, but those traits could make communities susceptible to other disturbances and so could cause shifts in community composition due to anthropogenic climate change. To better understand the interactive influences of disturbance history and type on community composition, we investigated the response of macroinvertebrate communities to disturbance using in-stream channels. Using a split-plot design, individual channels in five 'stable' streams and five 'frequently disturbed' streams (disturbance history) were subject to different disturbance type treatments (flooding, drying and a control). Disturbance type independently drove effects on species diversity, but all other effects of disturbance type depended on disturbance history. In particular, the interaction of disturbance type and history determined overall community response. Both disturbance types tested produced similar community responses in frequently disturbed streams, including changes in community composition and alterations to the abundance of less mobile taxa, but low-flow had a significantly greater effect in stable streams. Macroinvertebrate drift was greatest in the rock-rolling treatments and significantly less in the low-flow treatment for both disturbance histories. Therefore, disturbance history moderated the effects of disturbance type and determined the mechanism of community response by determining how well species were adapted to disturbance. This outcome suggests that previous disturbances strongly influence how vulnerable communities are to changes in disturbance, and so should be considered when predicting how changes in disturbance regimes will affect future community composition.

**Keywords**

Disturbance, streams, channel experiment, resistance, resilience, species traits, drying, flooding, community composition

## Introduction

Many ecosystems face rapid shifts in environmental conditions (IPCC 2014, Mantyka-Pringle et al. 2014, Parmesan 2006). For example, climate change is predicted to increase the frequency of extreme events (Ledger and Milner 2015, Rahmstorf and Coumou 2011), and accelerate shifts in disturbance regimes (e.g. Tockner et al. 2010). Moreover, global change is also expected to increase the introduction of novel disturbances (Oki and Kanae 2006, Seidl et al. 2016), potentially modifying communities in unpredictable ways (e.g. Bogan and Lytle 2011, Occhipinti-Ambrogi 2007). Such changes to disturbance regimes are likely to have far-reaching implications for community assembly because disturbance is a key driver of composition (Lepori and Malmqvist 2009, Resh et al. 1988, Ricklefs 2004). Although current knowledge highlights disturbance as an important influence on community structure, understanding how the context of previous disturbance influences the ability of communities to respond to novel disturbances is lacking.

Disturbance refers to any event that changes biotic or abiotic conditions and results in the alteration of community structure or dynamics (Donohue et al. 2016). Importantly, disturbances directly shape communities through filtering communities for species with specific tolerance traits (Cornwell and Ackerly 2009, Death and Zimmermann 2005, Jacobsen and Dangles 2012). Species lacking such traits are unlikely to persist within frequently disturbed communities (Lebrija-Trejos et al. 2010, Poff 1997), so disturbance filters which species are able to colonize or persist (Vorste et al. 2016). Disturbance also introduces stochasticity by resetting communities and creating opportunities for species to

gain competitive advantages from recolonising habitats prior to others (Chase 2003, Death 2008). Finally, disturbance can also indirectly alter communities through mediating the effects of other processes, including biotic interactions (Chase 2007, Lepori and Malmqvist 2009, Menge and Sutherland 1987, Nyström and McIntosh 2003).

Different types of disturbance can also have contrasting influences on communities because they operate through different underlying mechanisms (Glasby and Underwood 1996, Lake 2000, Piggott et al. 2012). Pulse disturbances are sharply delineated, high-intensity, short-duration events, whereas press disturbances act on communities over longer time periods (Lake 2000). In streams, for example, flooding is a pulse disturbance associated with sudden displacement of individuals and resources leading to rapid shifts in community structure (Death 2008), whereas low-flow is a press disturbance leading to shifts in communities caused by changes in habitat size, physiochemical conditions and biotic interactions over longer time periods (Dewson et al. 2007). It can be expected that communities will display contrasting responses to different types of disturbance due to the dissimilar drivers.

Disturbance-driven selection for species traits also means that variation in how different types of disturbance affect communities will strongly influence the morphological and life-history characteristics of species. This selection allows species to respond to the type of disturbance they experience (Allison and Martiny 2008, Catford and Jansson 2014, Wootton et al. 1996), and over time the disturbance regime acting on a particular habitat can act as a template to facilitate the evolution of traits that enable species to persist within that location (the 'habitat template of disturbance'; Townsend et al. 1997). Well-adapted species can persist following disturbance through either being resistant or resilient to disturbance events (Allison and Martiny 2008, Lake 2013, Robson et al. 2011). ‘Resistance’ is the ability to withstand disturbance and ‘resilience’ is the

ability to recover following disturbance (Pimm 1984), but both are connected to community stability (Donohue et al. 2013). For example, streamlined body shapes and the use of flow refugia allow aquatic macroinvertebrate species to resist flooding disturbances, while high vagility and rapid reproduction allow species to recolonise habitats quickly and so be more resilient to disturbance (Holomuzki and Biggs 2000), with both responses contributing to overall ability of communities to persist following disturbance ('ecological resilience'; Nimmo et al. 2015). Importantly, the combination of traits that confer resistance and resilience to disturbance can differ across disturbance types (Ledger et al. 2011, Lytle and Poff 2004). Therefore, species adapted to one type of disturbance may not be able to persist if subjected to other types of disturbance.

In addition to disturbance type, disturbance frequency or the pattern of disturbances experienced over time (disturbance history) also strongly influences communities (Jacobsen and Dangles 2012, McCabe and Gotelli 2000, Ward 1998). Increased disturbance frequency not only increases the effect of disturbances on communities and alters community interactions (Death 1996, Peckarsky et al. 2015), but also creates stronger selection for disturbance-adapted traits (Cornwell and Ackerly 2009, Lytle and Poff 2004, Townsend and Hildrew 1994). Thus, frequently disturbed communities should be better able to respond to types of disturbance they regularly experience compared to communities with benign environmental conditions.

Communities subject to frequent disturbances may be less affected by novel types of disturbance if their history of previous disturbance results in selection for traits suited to variable environmental conditions (e.g. high mobility, rapid reproduction; Holomuzki and Biggs 2000), and more strongly filtered communities (Fattorini and Halle 2004). However, the opposite could also be true depending on how novel new disturbances are and the generality of disturbance responses across taxa (Vinebrooke et al. 2004). Additionally, the

lower species diversity and reduced complexity often associated with frequently disturbed communities may also reduce community stability over longer time periods (Bogan et al. 2015, Death and Winterbourn 1995, Gray et al. 2006), potentially undermining the ability of frequently disturbed communities to withstand novel disturbances (Didham et al. 2005). The response of communities to disturbance is also influenced by the interaction of disturbance history with other community structuring processes (Chase 2007, Peckarsky et al. 2015, Thompson and Townsend 2006), and trade-offs between biotic processes and disturbance, such as species displaying different trait combinations as the strength of selection for disturbance-adapted traits varies (Chase 2007, Wellborn et al. 1996). For example, disturbance commonly selects for increased mobility, while predation selects for physical defences (Wellborn et al. 1996, Wootton et al. 1996). Thus, communities experiencing one type of disturbance may not have appropriate traits to respond to other, unfamiliar, disturbance types. Furthermore, because traits cannot respond to rapid or short-term changes in disturbance or other community processes (Lytle et al. 2008), changes in disturbance type could severely affect communities with a history of experiencing different types of disturbance. Therefore, there are many reasons to expect disturbance history to interact with disturbance type.

We carried out an experiment to investigate how disturbance history influenced the response of stream communities to different types of disturbance. We expected communities previously subject to frequent disturbances to be more resistant to further disturbance compared to communities in stable environments, due to stronger selection for species displaying resistance traits. We also expected frequently disturbed communities to display a smaller response to a different type of disturbance because species in frequently disturbed communities were more likely to display traits already adapted to respond to

disturbance compared to communities in stable environments, and often fewer sensitive species are present within frequently disturbed communities.

## Materials and methods

To investigate how disturbance type and history affected macroinvertebrate communities, we ran a field experiment between December 2016 and March 2017 in ten streams in the Upper Waimakariri River catchment, on the eastern slopes of the Southern Alps in Canterbury, New Zealand using in-stream channels as experimental units (Supplementary material Appendix 1, Table A1). Our experiment was timed to coincide with stable summer flows, however some streams were subjected to a typical summer flood prior to the experiment. All experimental locations had perennial flow, were 550 - 750 m above sea level, and flowed through tussock grasslands or scrub with some southern beech forest in their headwaters. Fish were present in all sites and had access to channels during colonization.

To test the effect of disturbance history, streams were categorised as either having a history of frequent flooding disturbance or a stable disturbance history (n=5 for each; Supplementary material Appendix 1, Table A1). Categories were based on previously described disturbance histories (Death and Winterbourn 1995, Jellyman et al. 2013), ground-truthed using the Pfankuch river disturbance index (RDI; Pfankuch 1975). The RDI incorporates 15 different visually-estimated characteristics of upper bank, lower bank, and stream bed characteristics to produce an overall score of physical channel stability (Jellyman et al. 2013, Peckarsky et al. 2014) strongly correlated with other measures of bed disturbance (Death and Winterbourn 1994, Jellyman et al. 2013, Peckarsky et al. 2014). By incorporating multiple characteristics of stream morphology, this also provides a measure of disturbance history over time, with high scores indicating more physically

147 unstable streams. Disturbed and stable streams had significantly different total RDI scores
148 (disturbed: 106; stable: 45; ANOVA $P<0.001$, $F_{1,8}=225.8$; Supplementary material
149 Appendix 1, Table A1). Any confounding effect of location was avoided by using
150 disturbed and stable streams interspersed within the upper Waimakariri River catchment.
151 We used a split-plot design, whereby channels were placed in five stable streams
152 and five frequently disturbed streams (disturbance history 'plots'), and within each stream,
153 three channels were used to manipulate disturbance type. Treatments of disturbance type
154 were randomly allocated to individual channels within each stream, with one channel
155 retained as an undisturbed control. Disturbance type treatments included rock-rolling to
156 simulate the occurrence of flooding, as well as raising channels to create low-flow
157 conditions. Rock-rolling mimicked a frequent pulse disturbance affecting disturbed
158 streams that causes significant adverse effects on macroinvertebrate communities (Death
159 2008), but was not commonly experienced in the stable streams used. In contrast, low-flow
160 was chosen as press disturbance that was novel to both frequently disturbed and stable
161 streams. Disturbance type treatments were designed to match the characterisation of either
162 a pulse as a short-term and sharply delineated disturbance, or a press that reaches a
163 constant level that is maintained (Donohue et al. 2016, Lake 2000).
164
165 *Experimental setup*
166 Channels were installed adjacent to each other, parallel to the direction of flow in a
167 straight run with at least 20 cm of water depth (Supplementary material Appendix 1, Fig.
168 A1). Channels were constructed of half sections of Polyvinyl Chloride pipe, 1.5-m long
169 and 24 cm in diameter, as used by Nyström and McIntosh (2003). For this experiment,
170 channels were uncovered, with only a 20-mm lip and 6-mm stainless-steel mesh covering
171 the downstream end of each channel to prevent substrate being washed out while allowing

172 macroinvertebrates to disperse freely. Within each channel, open-topped plastic baskets
173 (24 x 12.5 x 6 cm) were used to retain cobble substrate and acted as standardised sampling
174 units. All channels were filled with equal quantities of clean gravel, with gravel particles
175 randomly chosen to ensure an assortment of particle sizes following Death (1996) and left
176 for 21 days following setup to allow macroinvertebrate colonization before disturbance
177 treatments were applied. Based on the known community composition of the streams used
178 by Nyström and McIntosh (2003), the macroinvertebrate communities within channels
179 were assumed to compare favourably to stream communities.
180 To simulate flooding in the rock-rolling treatment, all substrate particles within the
181 channel were vigorously rolled by hand for four minutes to replicate substrate movement,
182 as done by Nyström and McIntosh (2003). To ensure that rolling was spread equally across
183 the length of each channel, each substrate basket was rolled for 30 seconds, with the
184 remainder of time spread across the cobbles in-between baskets. Rock-rolling was
185 undertaken every four days over the five-week experiment. This duration and frequency of
186 rolling was chosen to increase the chance of observing a response in both frequently
187 disturbed and stable streams. Previous studies in the same catchment using artificial
188 substrate disturbance to replicate the effects of natural disturbance have shown that two
189 minutes of substrate disturbance was enough to displace macroinvertebrates (Nyström and
190 McIntosh 2003) and that macroinvertebrate communities in both stable and frequently
191 disturbed streams are adversely affected by artificial substrate movement (Death 1996).
192 The low-flow treatment involved raising channels out of the water to reduce depth to 2.5
193 cm to produce the reduced velocity and increased water temperatures characteristic of low-
194 flow conditions (Dewson et al. 2007; Supplementary materials, Table A2), as has been
195 done to investigate the longer term effects of drying (Ledger et al. 2011). It was impossible
196 to replicate all aspects of natural disturbance events like water discolouration prior to a

flood with our treatments. Nevertheless, our aim was to test community responses across contrasting disturbance histories and types, so we used treatments that could be consistently replicated across varied study sites. Moreover, our treatments consistently mimicked the major characteristics of the two disturbance types: bed movement and organism displacement for flooding, and severe reduction in discharge for low flow (Death 2008, Dewson et al. 2007). This is also in line with previous experiments indicating these types of manipulations can adequately capture the effects on aquatic macroinvertebrate communities of both types of disturbance tested (Ledger et al. 2009, Matthaei et al. 1997).

*Field sampling*

After applying treatments for five weeks, benthic macroinvertebrate communities were sampled by taking substrate baskets from each channel four days following the last disturbance. A randomly selected substrate basket was lifted into a 500-µm mesh net held immediately downstream, before rinsing the gravel through a 5-mm sieve to remove large gravel particles, with retained macroinvertebrates preserved in 70% ethanol for later processing.

In addition, dispersal out of channels during rock-rolling was measured with drift nets (30 x 15 cm opening, 1-m long, 250-µm mesh) placed directly behind each channel for the duration of rock-rolling treatment. Water flow through the drift nets (measured using a Marsh-McBirney Flomate Model 2000 Flowmeter), sampling duration and the depth of each net were used to calculate drift density using equation 1 from Allan and Russek (1985).

Physicochemical conditions were measured over the course of the experiment (Supplementary Material 1, Table A2). Water temperature was measured continuously in both the stream and low-flow treatment channel using HOBO (Onset Computer

Corporation) pendant loggers. Dissolved oxygen, as well as pH and specific conductivity were measured in each channel using handheld probes (YSI Ecosense ODO 200 and YSI Pro 1030, respectively).

*Laboratory methods*

Benthic samples taken from substrate baskets and drift samples taken during rock rolling were rinsed through a 500-µm sieve, separated from detritus, identified and counted under a dissecting microscope. With the exception of Chironomidae (identified to tribe/sub-class), Oligochaeta (sub-class), Nematoda (phylum) and Platyhelminthes (phylum), macroinvertebrate taxa were identified to genus following: Winterbourn et al. (2000), Smith (2003) and Smith (2003).

*Statistical analysis*

Community resistance to disturbance was tested using the difference between disturbance type and undisturbed control treatments. Non-metric multidimensional scaling (NMDS) and Bray-Curtis dissimilarity (Faith et al. 1987) were used to test for differences between disturbance history treatments (frequently disturbed and stable), and effects of different disturbance type within disturbance history. Significant differences in community composition were evaluated using a permutational analysis of variance (PERMANOVA, 999 permutations), with permutations restricted to combinations of disturbance history and type within each stream reflecting the split-plot design (Anderson 2001, Warton et al. 2012). Additionally, the absolute Bray-Curtis dissimilarity between the control and each type of disturbance within each stream was used to investigate how far community composition shifted with different types of disturbance (Faith et al. 1987) and tested using split-plot ANOVA. This allowed both the among-block effect of disturbance history, as

247 well as the within-block effect of disturbance type, and the interaction of disturbance
248 history and type to be tested.
249 To further elucidate community responses, diversity (calculated as 'effective
250 number of species'; Jost 2006), the relative abundance of snails (Potamopyrgus and Physa
251 spp.), cased Trichoptera species, and free-living taxa (i.e. lacking cases or shells) were also
252 tested using split-plot ANOVAs. Distinguishing shelled, cased and free-living taxa,
253 provided a coarse measure of how the abundance of mobile and less mobile species
254 changed (Death 1995, Wootton et al. 1996). Community responses were transformed into
255 log-response ratios by calculating the ratio of each disturbance type treatment response
256 relative to the control, and taking the natural log of this within each block (Hedges et al.
257 1999). The change in the relative abundance for each species group was calculated as the
258 difference in relative abundance between each disturbance type and the control treatment
259 within each stream, where relative abundance was the abundance of a group divided by
260 total abundance.
261 Finally, a split-plot ANOVA was used to evaluate differences in drift out of
262 channels during rock-rolling. For all analyses, assumptions of normality and homogeneity
263 of variance were tested using the Shapiro-Wilks test and the Levenes' Test respectively
264 and found to be satisfied. Statistical analyses were carried out using R statistical package,
265 version 3.2.5 (R Core Team 2016), with NMDS analyses and permutational analysis of
266 variance carried out using the vegan package (Oksanen et al. 2016).
267 **Results**
268 Habitat conditions and macroinvertebrate community composition were
269 significantly different between streams with a history of flooding compared to those not
270 subject to flooding (Figure 1, PERMANOVA, $F_{1,24}$=3.288, P=0.003). Across disturbance
271 histories, water depth was greater in stable streams, while temperature was higher in

272 frequently disturbed streams and there was no difference in flow velocity (Table A2). In
273 macroinvertebrate communities, *Deleatidium* spp mayflies, Hydrobiosidae and
274 Hydroptilidae caddisflies, and Orthocladiinae fly larvae were most prevalent in frequently
275 disturbed streams, with Oligochaeta and Plecoptera (including *Megaleptoperla* sp. and
276 Notonemouridae) also present. Stable streams were dominated by Trichoptera (especially
277 *Pycnocentrodes* sp.), Orthocladiinae and *Potamopyrgus* snails and also contained
278 *Austrosimulium*, Ostracoda, *Oxythira* and *Deleatidium*. Of taxa not identified to genus,
279 only Chironomidae were important components of communities (55% and 38% of
280 individuals in disturbed and stable communities, respectively). The low-flow treatment
281 caused significant reductions in channel flow velocity and depth, but had no effect on
282 water temperature, and there were no differences between habitat conditions in control and
283 rock-rolling treatment channels (Table A2).

284 Both rock-rolling and low-flow shifted community composition (Figure 1,
285 PERMANOVA, $F_{2,24}$=1.927, P=0.012), but there was no significant interaction between
286 disturbance type and disturbance history for overall composition (PERMANOVA,
287 $F_{2,24}$=1.017, P=0.417). When the change in composition between assemblages was
288 investigated using Bray-Curtis dissimilarity, the effect of disturbance type was dependent
289 on disturbance history, indicated by a significant disturbance history by type interaction
290 (Figure 2, Table 1a). In stable streams, the low flow treatment altered community
291 composition more than rock-rolling and produced communities which diverged
292 substantially from control communities, whereas in frequently disturbed streams there was
293 no difference in the distance communities moved in ordination space in response to
294 different disturbance treatments (Figure 2).

295 Disturbance history and the type of disturbance experienced also drove changes in
296 total invertebrate abundance, diversity, and the abundance of different species groups with

297 different traits. Firstly, there was an interaction between disturbance type and disturbance
298 history affecting total invertebrate abundance (Table 1b, Figure 3a). In frequently
299 disturbed streams there was no significant effect of either rock-rolling or low-flow
300 disturbance on total abundance (Figure 3a), whereas in stable streams, both rock-rolling
301 and low flow significantly reduced total invertebrate abundance, with low flow having a
302 greater effect (Figure 3a).

303 In contrast to total abundance, only disturbance type affected diversity, regardless
304 of disturbance history, because rock-rolling decreased diversity in both frequently
305 disturbed and stable streams (Table 1c, Figure 3b). However, when split into species
306 groups based on mobility-related traits – including snails (*Potamopyrgus* and *Physa*),
307 cased Trichoptera species (e.g. *Hudsonema* and *Pycnocentrodes*) and free-living (i.e.
308 lacking cases or shells) taxa – the influence of both disturbance type and history varied
309 (Figure 4). Firstly, the effect of different types of disturbance on the relative abundance of
310 snails was dependent on disturbance history (Table 1d). Snails were not present in
311 frequently disturbed streams, and so could not be affected by further disturbance. In
312 contrast, rock-rolling significantly decreased the abundance of snails in stable streams,
313 while low flow had no significant effect (Figure 6a). The relative abundance of cased
314 Trichoptera spp. were also affected by an interaction between disturbance history and type.
315 Cased Trichoptera significantly decreased in relative abundance following both
316 disturbance treatments in stable streams, whereas in frequently disturbed streams, the
317 relative abundance of cased Trichoptera did not change significantly regardless of
318 disturbance type (Table 1e, Figure 4b). This was likely due to cased Trichoptera either
319 being absent or in very low abundances in frequently disturbed streams. Finally, the
320 relative abundance of free-living taxa was also dependent on an interaction between
321 disturbance history and type because although further disturbance had no effect on the

322 relative abundance of free-living taxa in frequently disturbed streams, it had a significant
323 positive effect on relative abundance in stable streams regardless of disturbance type
324 (Table 1e, Figure 4c).

325 The drift of individuals out of channels during disturbance treatments was
326 significantly affected by disturbance type, but not disturbance history (Table 1g, Figure 5).
327 In both frequently disturbed and stable streams, rock-rolling increased the movement of
328 invertebrates out of channels, while low flow significantly decreased invertebrate drift
329 (Figure 5). The change in invertebrate drift relative to the control treatment differed
330 slightly between frequently disturbed and stable streams, with low flow decreasing
331 invertebrate drift significantly in frequently disturbed streams, while rock-rolling
332 significantly increased the movement of invertebrates out of channels in stable streams.
333 However, there was no significant effect of disturbance history on the loss of invertebrates
334 out of channels because the difference in invertebrate drift between disturbance treatments
335 remained constant (Table 1g). Therefore, disturbance type had the strongest influence on
336 the movement of invertebrates in the experiment.

337 **Discussion**

338 Differences in disturbance characteristics experienced by communities (Miller et
339 al. 2011) and the legacies of previous perturbations (Peckarsky et al. 2015, Sylvain et al.
340 2012) likely alter the effects of disturbance on communities. Thus, developing a more
341 nuanced understanding of how different aspects of disturbance interact is important for
342 understanding how changes in disturbance regimes will alter community composition. Our
343 experiment demonstrated that different aspects of disturbance influence how stream
344 macroinvertebrate communities respond to disturbance. Whether communities in
345 frequently disturbed streams displayed a similar response to further disturbance compared
346 to communities in stable streams was often determined by the type of disturbance.

Community responses to rock-rolling differed little between disturbance histories, but the effects of the low-flow treatment differed between disturbed and stable streams. Specifically, the low flow treatment had greater effects on macroinvertebrate communities in stable streams compared to those in frequently disturbed streams. Therefore, the interactions between the effects of disturbance type and history suggest that the effects of different types of disturbance on community composition are contingent on previously experienced disturbance. Below we outline important aspects of these relationships, starting with effects of disturbance history on community composition.

Across all streams, community composition differed significantly between contrasting disturbance histories, with mobile species such as mayflies most prevalent in frequently disturbed rivers, whereas stable streams were dominated by species protected by shells or cases like snails and cased Trichoptera. Overall, there was a distinct difference in community composition between disturbance histories, as well as significant shifts in composition following disturbance treatments. This aligns with previous work demonstrating that differences in community composition reflect local disturbance history (Gray et al. 2006, Jacobsen and Dangles 2012), due to disturbance filtering out ill-adapted species (Lebrija-Trejos et al. 2010). Except for changes in the relative abundance of free-living mobile invertebrate taxa, all benthic community response metrics were negatively affected by disturbance treatments. Therefore, our findings support the expectation that disturbance exerts strong influence on aquatic communities (Resh et al. 1988), that disturbance shapes community composition by filtering communities (Fattorini and Halle 2004), and that such effects can be evaluated with small-scale experiments such as ours (Ledger et al. 2009, Matthaei et al. 1997).

Our results highlight that disturbance history and the type of disturbance experienced affected community responses differently. Statistically significant interactions

were recorded for most response variables tested, but only a significant main effect of disturbance type influenced Shannon-Wiener diversity. Thus, disturbance type was a key aspect determining whether species were completely removed by disturbance, as observed from the effects of other environmental stressors (Matthaei et al. 2010). Rock-rolling noticeably removed species, indicated by the decline in Shannon-Wiener diversity. By comparison, diversity did not significantly change when communities were subject to the low-flow conditions we imposed. Rock-rolling associated with flooding displaces both macroinvertebrates and resources from the substratum (Death and Zimmermann 2005), removing species unable to remain attached to cobbles or recolonize rapidly (Holomuzki and Biggs 2000). In contrast to rock-rolling, low-flow disturbance likely had little effect on diversity because many species were better adapted to persist when subject to low-flow conditions, or because the low-flow treatment used in the experiment was not severe enough to remove species.

The most common interaction between disturbance history and type occurred because frequently disturbed streams responded to both rock-rolling and low flow similarly, whereas in stable streams responses to low flow were greater than those for rock-rolling. This was evident for both the differences in community composition and the changes in total abundance. Changes in the type and frequency of disturbance experienced previously (i.e. disturbance history) were expected to change which species were filtered out of communities and the harshness of the disturbance filter because disturbance-adapted traits can facilitate species, and therefore community, resistance to disturbance, preventing species from being removed by further disturbance ((Death 1996), Holomuzki and Biggs 2000, Fattorini and Halle 2004). In frequently disturbed communities, original community diversity was lower and species were likely already disturbance-resistant (Scarsbrook and Townsend 1993), potentially explaining their lesser responses to additional disturbance.

397 The importance of species traits in communities with different disturbance histories
398 in underpinning these different responses to disturbance types was shown by changes in
399 the relative abundance of snails, cased Trichoptera and free-living taxa. There was no
400 significant effect of either disturbance type on the relative abundance of snails in
401 frequently disturbed streams because snails were absent from these streams, while just
402 rock-rolling had a significant negative effect on snails in stable streams. Thus, species with
403 unsuitable traits were already filtered out of disturbed streams, due to being adapted to
404 avoid predation through protective shells rather than being tolerant of disturbance
405 (Wootton et al. 1996). Both types of disturbance investigated adversely affected cased
406 caddisflies, but cased caddisflies declined more in stable streams compared to frequently
407 disturbed streams. However, cased caddisflies were actually rare in frequently disturbed
408 sites, so similar to snails, additional disturbance could not decrease their abundance
409 further. In contrast, the free-living taxa like mayflies which were dominant in frequently
410 disturbed streams were not affected by either disturbance type in frequently disturbed
411 streams, likely due to high dispersal ability associated with their streamlined body shapes
412 (Holomuzki and Biggs 2000). Thus, previously disturbed environments likely contained
413 communities that were already generally resistant to disturbance, which is likely to be a
414 powerful mechanism controlling responses to additional types of disturbance.
415 Although resistance traits were important, stable streams responding more to low-
416 flow disturbance than frequently disturbed streams suggests that other traits also affected
417 community responses. Dispersal traits enable species to persist within communities
418 following disturbance through recolonization (Datry et al. 2014), and so the supply of
419 colonists influences recovery following disturbance (Catford and Jansson 2014, Datry et
420 al. 2016). In our experiment, low flow had stronger effects in the more diverse stable
421 communities, potentially due to weaker connections with sources of colonists from

422 reduced water flow (Bogan and Lytle 2011). Moreover, traits contributing to both
423 resistance and resilience responses are affected by previous disturbance history (Lytle and
424 Poff 2004, Bogan et al. 2015), so the dominance of stable communities by less mobile taxa
425 likely reduced community resilience. Thus, disturbance history and the type of disturbance
426 experienced also likely interact to affect how communities respond to disturbance
427 communities by influencing species mobility.

428 Invertebrate drift samples collected during rock-rolling showed that dispersal out of
429 rolled channels was significantly greater than drift out of low-flow channels in both
430 disturbance histories. Despite considerable drift out of channels subject to rock-rolling, the
431 effect of rock-rolling on total macroinvertebrate abundance and community dissimilarity
432 for benthic communities was smaller than the effect of low flow in stable streams. This
433 implied that communities from both frequently disturbed and stable streams subjected to
434 rock-rolling recovered during the interval between rock-rolling and benthic communities
435 being sampled, whereas stable stream communities did not recover from low flow. Rock-
436 rolling was a pulse disturbance occurring as multiple discrete events, providing the
437 opportunity for communities to recover between disturbances through recolonization by
438 mobile species (Donohue et al. 2016). By comparison, low flow is a press disturbance
439 which reduces recolonization potential through the reduction of water flow. Furthermore,
440 rapid recolonization of communities within instream channels has been demonstrated for
441 less intense rock-rolling disturbances (Nyström and McIntosh 2003), with greater
442 recolonization likely in stable environments due to greater availability of colonists than in
443 frequently disturbed environments (Chase 2003). Therefore, while we did not explicitly
444 quantify community resilience, it appears that disturbance history moderated the effect of
445 disturbance type by influencing community resilience through the availability of new
446 colonists and the dispersal traits of species present.

447 The interaction of disturbance history and type, especially that affecting overall
448 community composition measured by Bray-Curtis distance, is consistent with both
449 disturbance tolerant and mobility traits contributing to community responses to disturbance
450 through enabling species to withstand disturbance events and recolonize following
451 disturbance (Catford and Jansson 2014, Vorste et al. 2016). These mechanisms operated
452 together because when communities lacked resistance traits, as in stable streams,
453 community structure was most affected by a type of disturbance, low flow, which hindered
454 recolonization. Likewise, recolonization appeared less essential for communities with
455 resistance traits in the disturbed streams, because the effect of disturbance was less and
456 fewer species were lost. This interplay of different responses to disturbance corresponds to
457 those observed in other ecosystem types, including grassland and intertidal algal
458 communities, where resilience becomes a key response once the capacity of species to
459 resist disturbance is exhausted (Allison 2004, Hoover et al. 2014). Thus, disturbance
460 history moderates the effect of disturbance type by driving the development of disturbance
461 resistance traits and traits which are likely to affect resilience such as increased mobility.
462 The involvement of both resistance traits and resilience responses through species
463 mobility reflects the multiple interrelated components of overall community stability
464 (Donohue et al. 2013). Therefore, the nuances of how different aspects of disturbance
465 influences communities are important for understanding how historical context influences
466 the effects of disturbance on communities, and thus how changes in disturbance regime
467 might alter communities. In the context of global change, the role of disturbance history in
468 moderating the effect of disturbance type on freshwater macroinvertebrates provides an
469 important insight into the role of different aspects of disturbance in shaping communities
470 and so whether different communities are more vulnerable to changes in disturbances. Our
471 findings suggest important disturbance responses are associated with dispersal ability and

mobility by allowing species that are not disturbance-adapted to respond to disturbance and so facilitates a degree of resilience. This drove the interaction between disturbance history and type, because non-disturbance adapted communities were still equally able to respond to disturbance provided species mobility allowed dispersal into disturbed areas (i.e., not impeded by low flow). While both resistance and resilience responses were evident in our experiment, we would expect that the importance of resistance responses increases with more severe drying disturbance as habitat connectivity declines and dispersal benefit of greater mobility decreases as streams dry up (Bogan and Lytle 2011).

Making predications for how vulnerable communities are to new or novel disturbances is complicated by the consideration of disturbance magnitude and duration (Donohue et al. 2016), as well as spatial scale (Matthaei et al. 1997). The effects of disturbance history may also be more pronounced in ecosystems with predictable disturbance regimes, because the highly variable disturbance regimes of New Zealand freshwater ecosystems drives selection for resilience traits and limits the evolution of specialized disturbance resistance traits (Clausen and Biggs 2000, Wissinger et al. 2009). This probably means that our results emphasize the importance of resilience for community responses to disturbance and may understate the importance of resistance traits for responding to specific disturbance types. Therefore, disturbance history will likely provide valuable insight into how vulnerable communities are to changes in disturbance patterns arising from global change. Moreover, that communities in stable environments are more vulnerable to changes in a region where the regional species pool is characterised by high resilience like New Zealand suggests that general adaptation to disturbance alone may be insufficient to respond to shifting disturbance regimes. Thus, environments with less history of disturbance will be more vulnerable to changes in disturbance regimes and

496 novel disturbances, and these environments may warrant greater management effort to
497 limit the effects of global change.
498

## Declarations

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**Conflicts of interest:** The authors declare that they have no conflicts of interest.

**Data availability:** The data presented in this paper will be made available on Dryad when accepted for publication.

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702

**Table 1**: Results of ANOVAs to test effects of disturbance history and disturbance type for Bray-Curtis community dissimilarity (a), total invertebrate abundance (b), Shannon-Weiner diversity (c), relative abundance of snails (d), relative abundance of cased Trichoptera (e), relative abundance of free-living taxa (f) and drift during rock-rolling (g).

| | d.f. | SS | F | P |
|---|---|---|---|---|
| **a) Bray-Curtis community dissimilarity** | | | | |
| History | 1 | 0.03 | 0.69 | 0.43 |
| Residual (sites) | 8 | 0.33 | | |
| Type | 1 | 0.04 | 4.92 | 0.057 |
| History*type | 1 | 0.99 | 11.42 | 0.009 |
| Residual (within sites) | 8 | 0.07 | | |
| **b) Total invertebrate abundance** | | | | |
| History | 1 | 5.21 | 2.17 | 0.179 |
| Residual (sites) | 8 | 0.33 | | |
| Type | 1 | 0.86 | 3.33 | 0.105 |
| History*type | 1 | 2.01 | 7.82 | 0.023 |
| Residual (within sites) | 8 | 0.04 | | |
| **c) Effective number of species** | | | | |
| History | 1 | 0.24 | 1.83 | 0.213 |
| Residual (sites) | 8 | 1.06 | | |
| Type | 1 | 0.75 | 9.53 | 0.015 |
| History*type | 1 | 0.01 | 0.13 | 0.725 |
| Residual (within sites) | 8 | 0.63 | | |
| **d) Snails** | | | | |
| History | 1 | 0.01 | 0.44 | 0.525 |
| Residual (sites) | 8 | 0.08 | | |
| Type | 1 | 0.02 | 10.76 | 0.011 |
| History*type | 1 | 0.02 | 10.17 | 0.013 |
| Residual (within sites) | 8 | 0.02 | | |
| **e) Cased Trichoptera** | | | | |
| History | 1 | 0.18 | 9.59 | 0.014 |
| Residual (sites) | 8 | 0.15 | | |
| Type | 1 | 0.01 | 0.82 | 0.390 |
| History*type | 1 | 0.02 | 1.13 | 0.319 |
| Residual (within sites) | 8 | 0.11 | | |
| **f) Free-living taxa** | | | | |
| History | 1 | 0.24 | 14.37 | 0.005 |
| Residual (sites) | 8 | 0.14 | | |
| Type | 1 | 0.01 | 0.12 | 0.738 |
| History*type | 1 | 0.07 | 5.68 | 0.044 |
| Residual (within sites) | 8 | 0.10 | | |
| **g) Rock-rolling drift** | | | | |
| History | 1 | 5.46 | 2.86 | 0.129 |
| Residual (sites) | 8 | 15.29 | | |
| Type | 1 | 54.66 | 6.99 | 0.01 |
| History*type | 1 | 0.54 | 0.48 | 0.51 |
| Residual (within sites) | 8 | 22.62 | | |

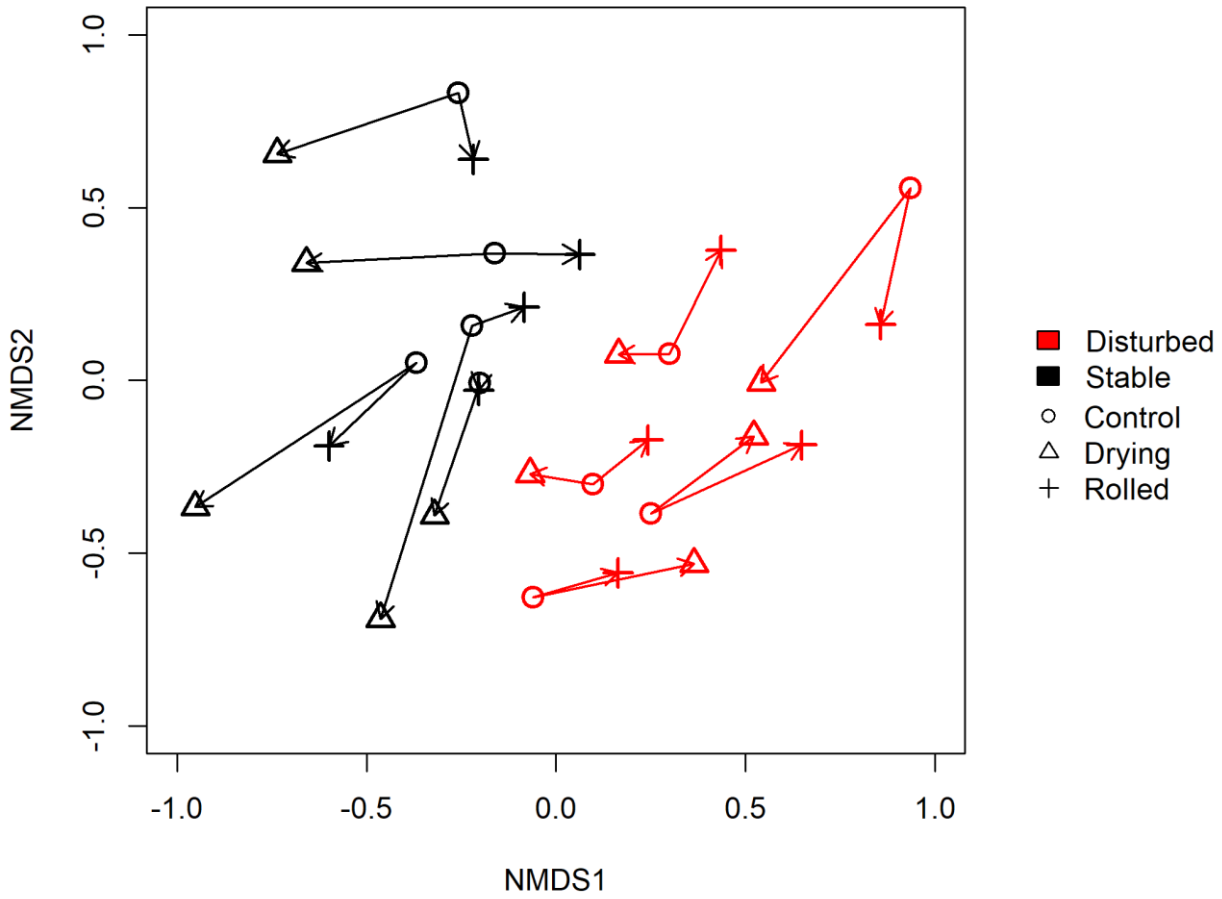



**Figure 1:** Non-metric multidimensional scaling plot of Bray-Curtis dissimilarity in stream macroinvertebrate assemblages across channels in streams with different disturbance histories (colours) subject to different types of disturbance (symbols). Points represent assemblages in individual channels, with arrows connecting control channels (circles) with channels subject to low-flow (triangles) and rock-rolling (plus) disturbances within the same stream.

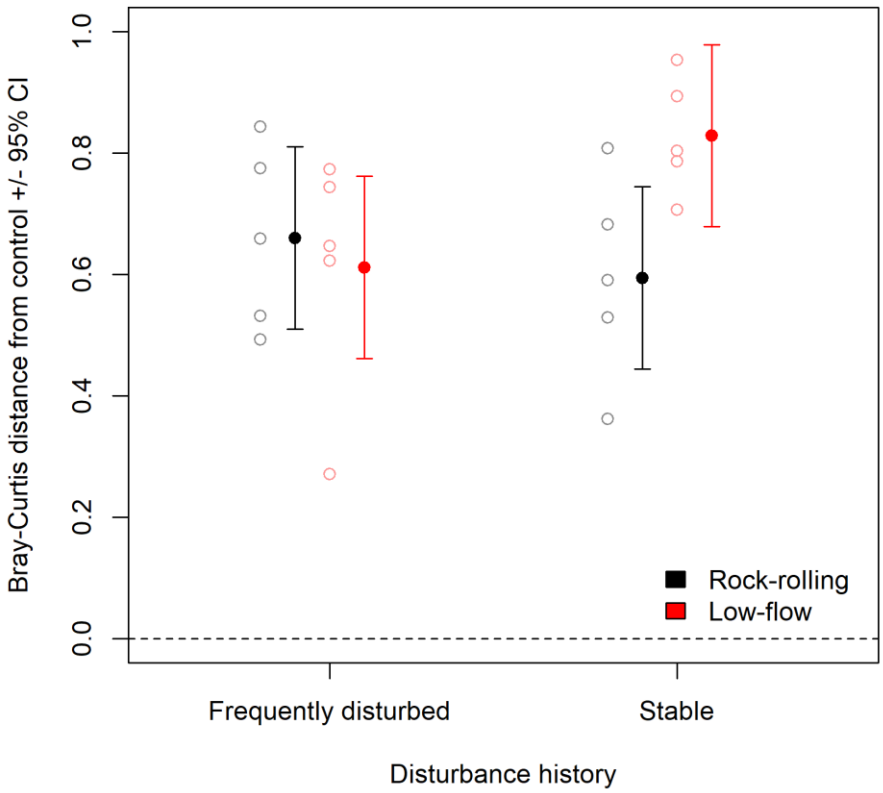
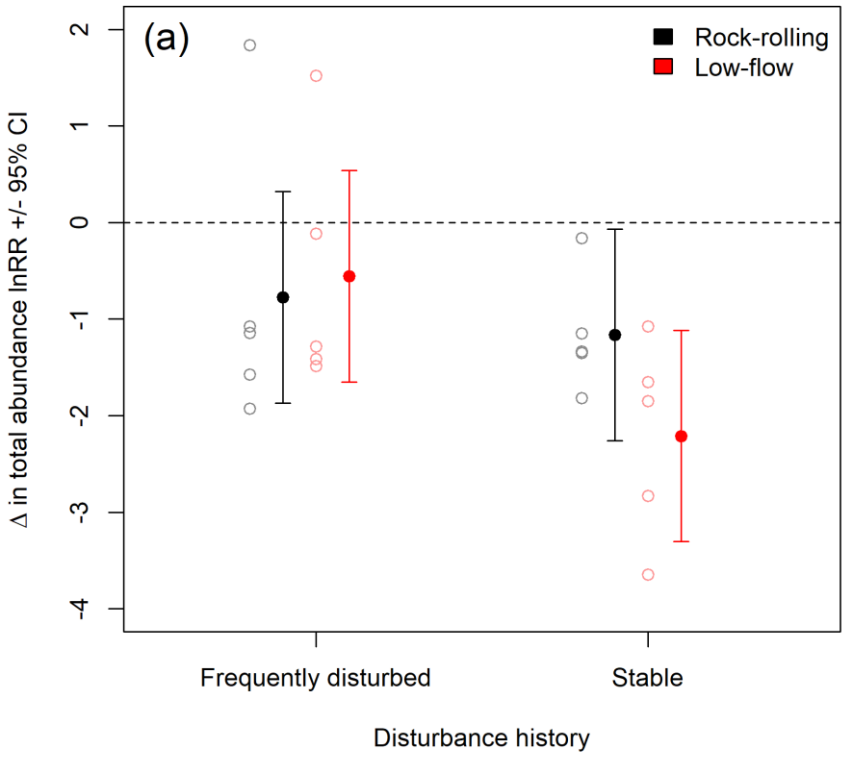



**Figure 2:** Mean Bray-Curtis dissimilarity of macro-invertebrate communities between control channels and channels subject to different types of disturbance for each category of disturbance history (±95% CI). Black points indicate the effects of rock-rolling, while red points indicate the effects of low-flow disturbance and open points indicate raw values from each replicate. The dashed zero line represents the control treatment, and therefore any 95% CI's overlapping the dashed line show a non-significant effect size.


(a)
Rock-rolling
Low-flow
Δ in total abundance lnRR +/- 95% CI
2
1
0
-1
-2
-3
-4
Frequently disturbed
Stable
Disturbance history

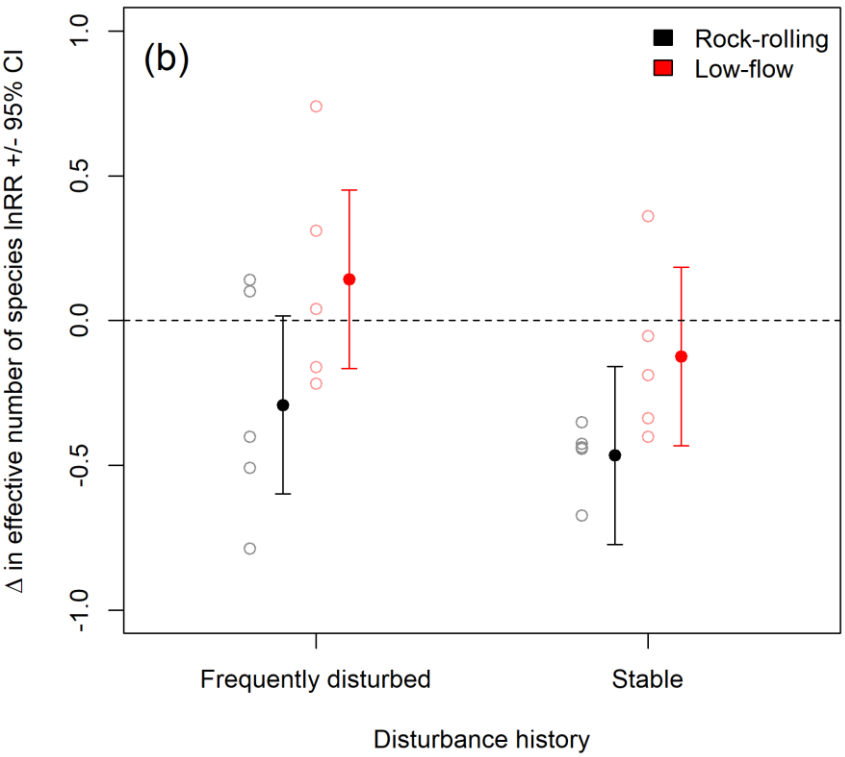
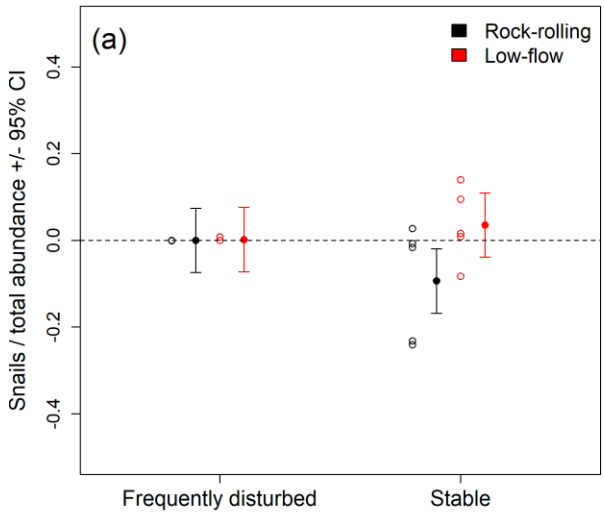
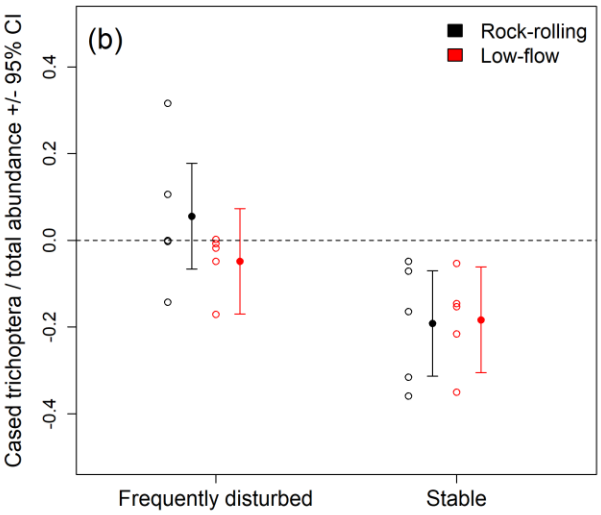

(b)
Rock-rolling
Low-flow
Δ in effective number of species lnRR +/- 95% CI
1.0
0.5
0.0
-0.5
-1.0
Frequently disturbed
Stable
Disturbance history

**Figure 3:** Mean $\log_e$ response ratios of the difference in (a) total macroinvertebrate abundance and (b) the effective species diversity of macroinvertebrate communities, between control channels and channels subject to different types of disturbance for each category of disturbance history (±95% CI). Black points indicate the effects of rock-rolling, while red points indicate the effects of low-flow disturbance and open points indicate raw values from each replicate. The dashed zero line represents the control treatment, and therefore any 95% CIs overlapping the dashed line show a non-significant effect size.


(a)
Rock-rolling
Low-flow
Snails / total abundance +/- 95% CI
0.4
0.2
0.0
-0.2
-0.4
Frequently disturbed
Stable


(b)
Rock-rolling
Low-flow
Cased trichoptera / total abundance +/- 95% CI
0.4
0.2
0.0
-0.2
-0.4
Frequently disturbed
Stable

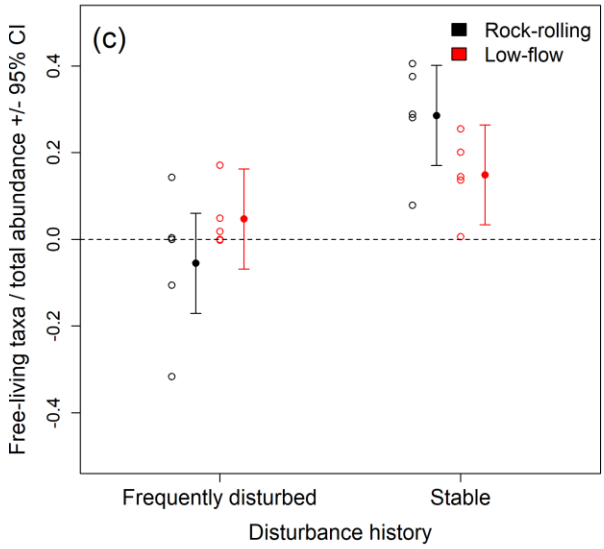

(c)
Rock-rolling
Low-flow
Free-living taxa / total abundance +/- 95% CI
0.4
0.2
0.0
-0.2
-0.4
Frequently disturbed
Stable
Disturbance history

**Figure 4:** Changes in the relative abundance of (A) snails, (B) cased Trichoptera and (C) free-living taxa with each disturbance type for each category of disturbance history (±95% CI). This was calculated as the difference in the proportion of total invertebrate abundance made up by each group between the control and each disturbance treatment, with axes multiplied by -1 so directions of change corresponded to the $\log_e$ response ratios presented in other figures. Black points indicate the effects of rock-rolling, while red points indicate the effects of low-flow disturbance and open points indicate raw values from each replicate. The dashed zero line represents the control treatment, and therefore any 95% CIs overlapping the dash line show a non-significant effect size.

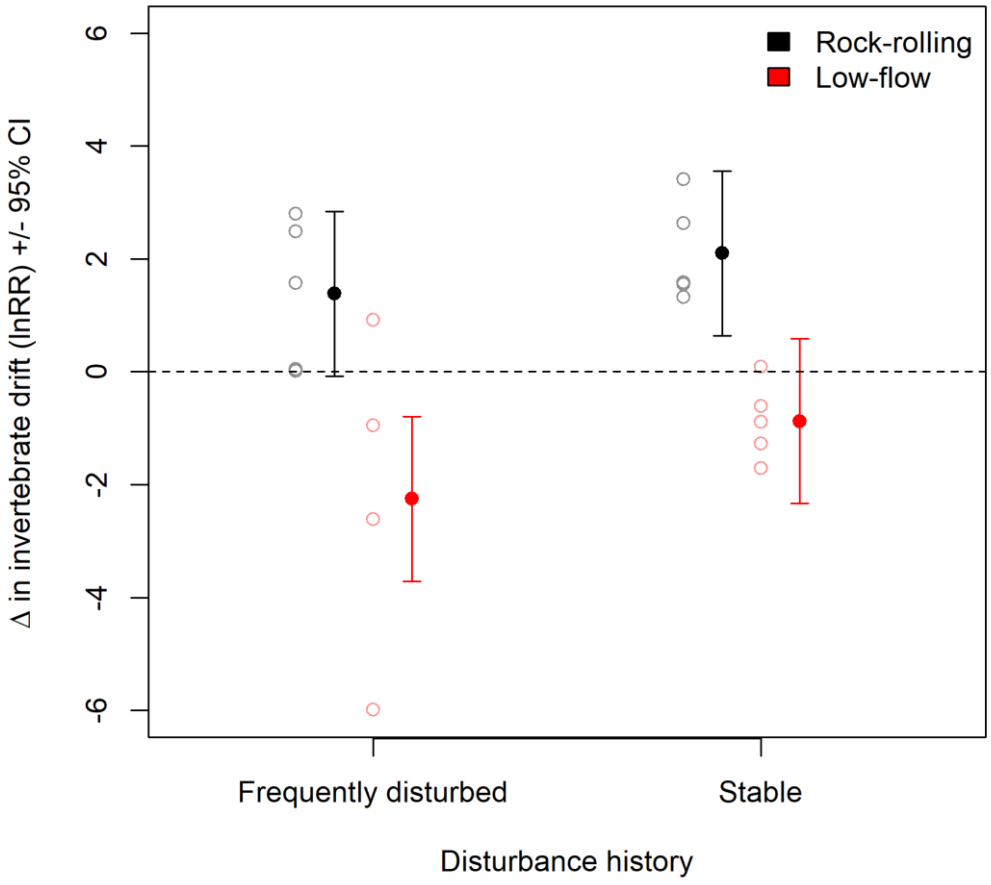



**Figure 5:** Mean $\log_e$ response ratios of the difference in invertebrate drift out of channels between control channels and channels subject to different types of disturbance during rock-rolling for each category of disturbance history (±95% CI). Black points indicate the effects of rock-rolling, while red points indicate the effects of low-flow disturbance and open points indicate raw values from each replicate. The dashed zero line represents the control treatment, and therefore any 95% CI's overlapping the dash line show a non-significant effect size.